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Aspects of Host Acceptance by *Pteromalus venustus* Walker and *Monodontomerus obsoletus* Fabricius, Parasitoids of *Megachile rotundata* (Fabricius), the Alfalfa Leafcutting Bee (Hymenoptera: Chalcididae)

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Abstract.—Preliminary experiments were conducted to: 1) determine the cues used by two species of chalcid parasitoids (*Monodontomerus obsoletus* [MO], *Pteromalus venustus* [PV]) to accept immature alfalfa leafcutter bees as hosts; and 2) compare the suitability and vulnerability to the parasitoids of different aged hosts. Initially, parasitoids accepted only fully authentic hosts. After 24 hours with hosts that were artificial in one or more respects, host acceptance behavior expanded to include some previously unacceptable hosts. However, the species differed in the kind of artificial hosts accepted with PV being more selective than was MO. All immature stages from prepupae to late pupae were acceptable as hosts to both species.

INTRODUCTION

Parasitoid wasps accept prospective hosts as food for rearing their offspring only after those hosts have satisfied a combination of stringent requirements. Stimuli that lead to oviposition by parasitoids can be physical or chemical and may include host size, shape, texture, activity and odor. The acceptance process, from host encounter to oviposition, is usually hierarchical and may consist of several steps (see Arthur 1981 for a review).

This report presents a preliminary description of host acceptance by two species of chalcid parasitoids. *Pteromalus venustus* Walker (Pteromalidae) and *Monodontomerus obsoletus* Fabricius (Torymidae) (subsequently referred to as PV and MO, respectively) were apparently introduced accidentally to North America with one of their several hosts, the alfalfa leafcutting bee (ALCB), *Megachile rotundata* (Fabricius). They are gregarious external parasitoids of the immature stages of bees and, perhaps some wasps, and can be abundant pests of the ALCB, the most important commercial pollinator of alfalfa, (*Medicago sativa* L.) in the Pacific northwest. The parasitoids immobilize the host by stinging and then deposit eggs between host and inner cocoon lining (Eves 1970, Hobbs and Krunic 1971). Immature individuals of any stage are vulnerable, but attack prior to the prepupal stage is usually fatal to both host and parasitoid offspring (Eves 1970). The eggs hatch in 36 to 48 hours and the first instar larvae begin to feed on the host. At 29°C, oviposition to adult eclosion takes about 21 days for MO (Eves 1970) and 12 days for PV (Whitfield and Richards 1985). Both species are multivoltine; individuals

overwinter as prepupae within host cocoons. (The species studied by Eves [1970] and Hobbs and Krunic [1971] was identified as *Monodontomerus obscurus* Westwood. Recent taxonomic work strongly suggests that *M. obsoletus* was actually the species studied [E. E. Grissell, pers. comm.; see below]).

Information was sought on two aspects of host acceptance/choice. First, the effect on host acceptance of manipulating several general characteristics of host larvae and cocoon was assessed. In the case of MO, these experiments both replicate and extend the work of Eves (1970). A second question, engendered by the more rapid developmental rates of parasitoids than hosts, relates to the suitability of ALCB pupae as hosts. When ALCB prepupae are incubated by beekeepers in anticipation of alfalfa bloom in late spring/early summer, adult parasites emerge first and may then attack other unparasitized, maturing ALCBs. Thus, it is of interest to determine if developing bee pupae of different ages are as attractive and suitable as hosts as are the more commonly parasitized prepupae.

Methods

All experiments were conducted using freshly emerged, unfed parasites from stock populations maintained at this laboratory. ALCB prepupae were removed from overwinter storage at 4–5°C and held at room temperature (~25°C) for 24 hours before being used in experiments. Experiments were conducted in clean glass petri dishes at 29°C and 16L:8D photoperiod.

To determine the importance of the cocoon and prepupae, 10 to 20 females of each species were each isolated with two specimens of one of the following five types of "host" until they either oviposited or expired: a) unencased (naked) ALCB prepupae; b) ALCB cocoons from which the prepupae had been removed through a partial slit at one end; c) ALCB prepupae inside #2 gelatin capsules; and, agar "prepupae" inside either d) empty ALCB cocoons slit as in (b), or e) #2 gelatin capsules. Hosts encased by cocoons or #2 gelatin capsules (18mm × 6mm) were fixed to filter paper in the bottom of the dishes by applying a small drop of non-toxic glue to the encasement. Unencased hosts, i.e., naked larvae, were not anchored to the substrate. Care was taken to avoid handling the hosts. Artificial "bees" were made from plain agar in dimensions of leafcutter bee prepupae (8mm × 4mm diam.). Hosts were monitored several times each day to record the time and number of eggs laid.

The second part of the study was designed to compare acceptance and suitability of hosts at different developmental stages. Overwintering ALCB prepupae were removed from storage at 4–5°C and incubated at 29°C for 8 or 16 days (8D, 16D). Individual freshly emerged parasites were offered two hosts each from 8 day, 16 day and unincubated groups for 24 hours under 16L:8D photoperiod. To minimize effects of host size on acceptance, all prepupae were weighed and only those within 10% confidence limits of the mean were used for experiments. Hosts were incubated at 29°C for another 7 days and then cocoons were opened and the contents recorded.

Results

The majority of females of both species did not lay eggs in treatments in which either prepupae or cocoon were manipulated (Table 1). The only hosts parasitized by PV females were naked prepupae. Seven of 10 females parasitized the naked

prepupae, and those seven laid fewer eggs per host and took longer on average to lay them, than has been observed for unfed females (Tepedino 1987a, see below).

Naked prepupae (the only treatment accepted by PV females) were completely rejected as prospective hosts by female MO. All other host types were accepted by at least one female (Table 1). Significantly more prepupae in gelatin capsules were parasitized than any other treatment ($X^2 = 46.1$), d.f. = 1, $P < 0.001$); and significantly more agar "bees" in cocoons were parasitized than naked prepupae, empty cocoons and agar "bees" in gelatin capsules combined ($X^2 = 9.72$, d.f. = 1,

Table 1. Results of experiments on cocoon and host manipulations. Number of females tested, N = 10 for all but agar bees in gelatin capsules for *Monodontomerus* where N = 20.

	Monodontomerus				*Pteromalus*			
	Number		Mean (± SD)		Number		Mean (± SD)	
Treatment	♀♀ parasitizing	"Hosts" parasitized	First day oviposition	Eggs/ host	♀♀ parasitizing	"Hosts" parasitized	First day oviposition	Eggs/ host
naked prepupa	0	0	——	0	7	9	1.7 ± 1.1	7.1 ± 5.2
empty cocoon	1	1	4.0	7.0	0	0	——	——
prepupa/gel cap	9	17	2.9 ± 0.9	8.3 ± 3.6	0	0	——	——
agar bee/gel cap	3	4	2.0 ± 0.0	5.3 ± 3.9	0	0	——	——
agar bee/cocoon	6	8	1.33 ± 0.82	3.3 ± 1.5	0	0	——	——

Table 2. Number of females of MO and PV parasitizing over a 24-hour period, number of hosts parasitized, and mean number of eggs/host for three incubation treatments.

	Monodontomerus			*Pteromalus*		
	Number		Mean (± SD)	Number		Mean (± SD)
Treatment	Parasitizing	Hosts Parasitized	Eggs/ Host	Parasitizing	Hosts Parasitized	Eggs/ Host
Unincubated	22	27	3.8 ± 1.5	18	22	8.3 ± 5.2
8 D	27	47	4.1 ± 1.6	13	13	14.0 ± 6.0
16 D	26	42	4.1 ± 1.2	10	13	9.1 ± 4.5

$P < 0.005$). Females also deposited the most eggs per host in the treatment with the most acceptable hosts, i.e., prepupae in gelatin capsules.

Although MO females oviposited in three times as many hosts as did PV females, there is evidence they did so under duress. First, with the exception of the prepupa in gelatin capsules treatment, females rarely oviposited more than once; and second, the average time to initial oviposition was more than 48 hours after the experiment began. This is hardly typical behavior as unfed female MO commonly parasitize more than one host within the first 24 hours (Tepedino 1987a, b, see below).

In contrast to the outright rejections of, or reluctance to oviposit in, hosts that were artificial in some aspect, all developmental stages were accepted as hosts by both species of parasitoid within 24 hours (Table 2). However, the species differed in their acceptance criteria. MO females oviposited significantly less frequently in unincubated cocoons than in 8D or 16D hosts ($X^2 = 7.9$, $P < 0.005$), but did not distinguish among treatments in the number of eggs laid per host (ANOV, $P > 0.50$). Conversely, PV females oviposited more frequently in unincubated hosts, but this distinction was not significant ($X^2 = 3.6$, d.f. $= 2$, $P > 0.10$). They did, however, lay significantly more eggs/host in 8D hosts than in the others.

Discussion

This study illustrates both the flexibility of host acceptance behavior in two parasitoid species and how those species may differ in the combination of cues used to accept a host individual. Initially, adult females of both species required that both cocoon and prepupae be authentic for a host to be accepted (Table 1). Unlike the prompt parasitization of authentic hosts of different developmental ages (Table 2), few artificial hosts were parasitized by any females of either species during the first 24 hours. Subsequently, PV females expanded their acceptance behavior, but only to include hosts in the naked prepupae category. The fact that authentic prepupae in gelatin capsules were ignored suggests that some characteristic of the cocoon other than size and shape is necessary for probing with the ovipositor to begin. Chemical and textural properties of the cocoon need to be examined.

In contrast, MO females were less selective in their behavior: after 24 hours, they began to accept hosts composed of a representative cocoon and prepupae so long as either of these was authentic. Thus, MO females replaced an obligatory initial requirement for cocoon and prepupal authenticity with a conditional requirement that only one be authentic. How "inauthentic" the artificial component of the cocoon-prepupal pair can be before becoming unstimulating or even repellent remains to be investigated as does the combination of cues that will support continued host investigation or oviposition. In any case, host acceptance behavior in MO appears to be more complicated than typical depictions of insect automatons reacting in simple concatenated sequences (Eibl-Eibesfeldt 1975).

Not only was the behavior of MO and PV females distinctive, but MO females treated empty cocoons differently from the behavior reported by Eves (1970). Largely because the females he observed invariably oviposited into empty cocoons, Eves (1970) concluded that the cocoon was the primary stimulus to oviposition and that the presence of a prepupae or larvae was of secondary importance. In contrast, none of the MO females in this study oviposited into empty cocoons and host acceptance seemed to depend on a complex interaction of individually flexible cues.

The most facile explanation for these differences is that Eves (1970) and I studied different species, but this seems improbable (E. E. Grissell, pers. comm.).

Both PV and MO also exhibited the ability to distinguish among authentic hosts of different developmental stages. Females of both species preferred immature stages of a particular (but different) age when given a choice. However, all stages from prepupae to late pupae were both acceptable and suitable. Unless appropriate control measures are taken (Richards 1984), unparasitized bees incubated for release into alfalfa fields are vulnerable to attack by female parasitoids which emerge well before maturing bees are ready to eclose.

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Literature Cited

Arthur, A. P. 1981. Host acceptance by parasitoids. Pp. 97–120 *in*: D. A. Nordlund, R. L. Jones and W. J. Lewis (eds.), Semiochemicals, Wiley & Sons, New York.

Eibl-Eibesfeldt, I. 1975. Ethology. Holt, Rinehart & Winston, New York.

Eves, J. D. 1970. Biology of *Monodontomerus obscurus* Westwood, a parasite of the alfalfa leafcutting bee, *Megachile rotundata* Fabricius (Hymenoptera: Torymidae; Megachilidae). Melanderia, 4:1–18.

Hobbs, G. A. and M. D. Krunic. 1971. Comparative behavior of three chalcidoid (Hymenoptera) parasites of the alfalfa leafcutter bee, *Megachile rotundata*, in the laboratory. Can. Entomol., 103:674–685.

Richards, K. W. 1984. Alfalfa leafcutter bee management in western Canada. Agriculture Canada Publication, 1495/E:53 pp.

Tepedino, V. J. 1987a. Notes on the reproductive biology of *Monodontomerus obsoletus, Pteromalus venustus*, and *Tetrastichus megachilidis*, three chalcid parasites of the alfalfa leafcutting bee, *Megachile rotundata*. Pan-Pac. Entomol., 63: (in press).

Tepedino, V. J. 1987b. Host discrimination in *Monodontomerus obsoletus* Fabricius (Hymenoptera: Torymidae), a parasite of the alfalfa leafcutting bee, *Megachile rotundata* (Fabricius) (Hymenoptera: Megachilidae). Ann. Entomol. Soc. Am. (in press).

Whitfield, G. H. and K. W. Richards. 1985. Influence of temperature on survival and rate of development of *Pteromalus venustus* (Hymenoptera: Pteromalidae), a parasite of the alfalfa leafcutter bee (Hymenoptera: Megachilidae). Can. Entomol., 117:811–818.